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Age Determination of Loggerhead Sea Turtles, *Caretta caretta*, by Incremental Growth Marks in the Skeleton

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Age Determination of Loggerhead Sea Turtles, *Caretta caretta*, by Incremental Growth Marks in the Skeleton

George R. Zug, Addison H. Wynn, and Carol Ruckdeschel

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ABSTRACT

Zug, George R., Addison H. Wynn, and Carol Ruckdeschel. Age Determination of Loggerhead Sea Turtles, *Caretta caretta*, by Incremental Growth Marks in the Skeleton. *Smithsonian Contributions to Zoology*, number 427, 34 pages, 9 figures, 6 tables, 1 appendix, 1986.—Periosteal growth in the skeleton of *Caretta caretta* is cyclic and produces a record of distinct bony layers (growth marks). These layers are most apparent in the long bones, particularly the humerus and femur. Correlative evidence supports the production of one layer (i.e., growth increment) each year in some reptiles, and the annual nature of each bony layer is an explicit assumption in our estimation of ages of *Caretta* from Cumberland Island, Georgia. Sections from the shafts of humeri were prepared with standard histological techniques, and the marks of skeletal growth were counted and measured. Owing to resorption of the early periosteal layers, determination of number of growth marks and, hence, age requires an extrapolation from the remaining marks to total growth marks produced during the life of the turtle. Various age estimates are possible; the most reliable are derived from the narrowest axis of the humerus sections and suggest that, on the average, Georgia *Caretta* attain sexual maturity in their thirteenth to fifteenth years, with some individuals possibly maturing as early as six years and others as late as their twenty-fifth year. Since the average age of maturity agrees with the results of a mark-recapture study in a neighboring Florida population, the value of the skeletochronological technique and its assumptions are confirmed. The technique is not advocated as a method for the age determination of individual sea turtles, but does provide statistical age estimates for different size classes of turtles.

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Dedicated to the memory of Chuck Ossola, a friend and outstanding scientific administrator. Chuck served as executive officer for the National Museum of Natural History from 1977 to 1982.

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Introduction

The "lost year" of sea turtles is much discussed. Upon entering the sea, what happens to the tiny hatchling sea turtles until they are seen again as half-grown juveniles? Where do they go, what do they do, and, most importantly, for how long are they absent? The intense and voluminous research efforts of the last decade and a half have slowly begun to answer these questions and have revealed many unanticipated and fascinating features of sea turtle biology, behavior, and ecology.

Of particular interest to us are growth rates, age at sexual maturity, and other aspects of aging. These aspects are critical in the development of demographic profiles for the different sea turtle species and populations, hence their conservation and management. Mark and recapture studies, such as those of Balazs (1980), Limpus and Walter (1980), and Mendonca (1981), are the ideal means for obtaining the most accurate age determinations. Such studies are, however, labor intensive, time demanding in the short and long term, and frequently logistically difficult and expensive. Captive-rearing, as done by Witham and Futch (1977) and Wood and Wood (1980), is similarly costly in time, labor, and equipment. Furthermore, captive rearing gives unnatural results, because these turtles grow faster and reach maturity sooner than wild ones (Balazs, 1979).

The research activities of the Université de Paris "Equipe de Récherche 'Formation squelettiques'" and particularly the investigations of Castanet into skeletochronology suggested an alternative approach that might convert the numerous strandings of dead sea turtles into potentially valuable research specimens. They (Castanet et al., 1970; Castanet, Meunier, and Ricqlès, 1977) provided a convincing argument that ectothermic vertebrates possess cyclic bone growth and that the cycles are annual. Other authors have offered varied opinions upon annual cyclic growth of bone in turtles. Mattox (1936) was the first to recognize the potential of bone growth rings or marks as a means of aging turtles; he noted that, in *Chrysemys picta*, smaller/younger turtles had fewer rings than did larger/older turtles. Peabody (1961) was a strong advocate of

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age determination through the use of these bony growth rings and he assumed, although he never tested, the annual nature of the rings. He observed these growth marks in *Chelydra serpentina*, but provided no estimate of age. Suzuki (1963) studied osteogenesis in *Trachemys scripta elegans*. He accepted the presence of annual growth layers in the long bones; however, he adamantly rejected the use of these growth marks for age determination owing to the extensive resorption and remodeling that occurs throughout growth. In contrast, Hammer (1969) suggested the use of the bony rings for aging, since he found a high correlation ($r = 0.94$) of number of rings to carapace length. Dobie (1971) found no such correlation in *Macroclemys temminckii*. He examined sections of vertebrae and mandibles, whereas Hammer used a variety of skeletal material, but found the growth marks most evident in long bones of *Chelydra*. Castanet and Cheylan (1979) found concordance between the number of rings and the known age of a *Testudo hermanni* and high correlations ($r = 0.89$) for ring number and carapace length (also scute annuli) in *T. graeca* and *T. hermanni*. Holm and Frazier (1979) also noted a positive relationship between number of bone layers and carapace length in several species of sea turtles. Castanet (1982) proposed that skeletochronology was promising for most turtles with the exception of sea turtles owing to the extensive remodeling in their long bones.

A number of amphibian and reptile species match age in years with number of bony growth layers. Hemelaar and van Gelder (1980) found that more than 90% of toads (*Bufo bufo*) recaptured showed an increase in number of marks of skeletal growth (MSGs) equal to the difference in years between capture and recapture. This concordance in a wild population is one of the strongest confirmations for the annual production of one growth layer in ectothermic tetrapods. Several studies by the Université de Paris research group (Castanet, Cheylan, de Buffrenil, Gasc, Meunier, Naulleau, and Pilorge) confirm the one-layer/one-year hypothesis. De Buffrenil (1980) showed that a 4-yr-old captive *Crocodylus siamensis* possessed three complete growth layers and was forming a fourth one at the time of its death. Castanet and Naulleau (1974) found that only 10% of their *Vipera aspis* born in captivity and raised under constant conditions match age and number of growth layers; in contrast, captive vipers exposed to seasonal conditions produced one growth layer per year. Pilorge and Castanet (1981, table 2) demonstrated complete agreement between actual age and number of growth layers. Minakami (1979) demonstrated that the growth period (deposition of a single zone) of *Trimeresurus okinavensis* occurred from June to September. His results derive from in vivo staining of snakes maintained in the laboratory. Similarly, Castanet (1982) showed with fluorescent labelling that one layer was deposited each year in *Lacerta viridis*. Studies of *Iguana iguana* (Zug, Rand, Wynn, and Bock, 1983) revealed that the number of growth layers closely match the known age of marked and recaptured animals.

Although numerous studies in turtles have confirmed the concordance of epidermal scute annuli with age in years, there is only one study with turtles of known ages that confirms the concordance of bone layer number with age in years. Castanet (1982) raised *Emys orbicularis* in seminatural conditions and with fluorescent labelling showed a one-to-one relationship between number of bone layers and years. Castanet and Cheylan (1979) demonstrated a concordance of epidermal scute annulus number with bony growth layers in *Testudo graeca* and *T. hermanni*; they also demonstrated a high positive correlation of skeletochronological age estimates and carapace length. Others (e.g., Hammer, 1969) have also observed a high correlation between carapace length and age estimates. The data confirming the production of one bone layer each year is largely circumstantial, but convincing. Herein, we summarize our successes and failures for age determination in the loggerhead sea turtle through the use of skeletochronology.

ACKNOWLEDGMENTS.—This research project had its beginning in a series of coincidences largely linked through Charles W. Potter.

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Shortly after G. Zug had read Castanet, Meunier, and Ricqlès (1977), C. Potter introduced him to Aleta Holm and her spinner dolphin aging research. Then after some tentative histological preparations of sea turtle bone proved successful, C. Potter introduced G. Zug to C. Ruckdeschel, thereby permitting the collection (Endangered Species Permit: PRT 2-2381) and eventual examination of a large, yet geographically restricted sample of sea turtles. C. Potter has our thanks for providing the initial linkage and stimulation for the research reported herein. The initial histological preparations were made by Margaret M. Barber; however, the histology for the research sample derives entirely from the skilled hands of Helen F. Wimer. Discussions on skeletochronology with Jack Frazier encouraged our research in the early stages. Nat Frazer and Terry Henwood most generously shared with us their current ideas and research data on *Caretta* growth and age determination.

The manuscript has benefitted by the reviews of Jacques Castanet, C. Kenneth Dodd, Jr., Nat B. Frazer, J. Whitfield Gibbons, Tyrell A. Henwood, W. Ronald Hever, Peter C.H. Pritchard, and Anders G.J. Rhodin. We appreciate their valuable advice, but remain totally responsible for the interpretations of the data.

This project was supported by the Smithsonian's Fluid Research Fund, NMNH Director's Fund, and the Department of Vertebrate Zoology. Without their support, this research would have been impossible.

Materials, Methods, and Rationale

TURTLES.—During 1979 and 1980, C.R. measured and collected a skeletal voucher specimen from each sea turtle stranded on the oceanic beach of Cumberland Island, Camden County, Georgia. A total of 187 *Caretta caretta* were stranded in 1979 (Ruckdeschel and Zug, 1980) and 222 in 1980 (Ruckdeschel and Zug, 1981). The preferred skeletal voucher was the complete cranial and right forelimb skeletons for each specimen. Many specimens, however, lacked appendages, head, or some combination thereof owing to butchery by original captors, sharks, or beachcombing souvenir hunters. Thus, our research samples are less than the total number of stranded turtles. The humeral morphometric set consists of 137 humeri, and the histological (age determination) set represents 119 humeri, in 81 of which MSGs could be measured. These sets derive almost entirely from the 1979 strandings.

SELECTION OF BONE.—Growth increments (= layers or marks) are observed most consistently in the long bones of turtles (see, e.g., Mattox, 1936; Hammer, 1969). Our preliminary histological examination included a third peripheral bone from the carapace, the dentary (a section adjacent to the symphysis and one in the middle of the ramus), a centrum of a cervical vertebrae, a penultimate phalanx of forefoot, an ulna, and a humerus. Regular periosteal layers were evident in the ulna and humerus. In the dentary, growth layers were present, but owing to the spongy nature of this bone, the layers were too irregularly arranged to permit accurate and repeatable counts and measurements. The peripheral bone, centrum, and phalanx showed no discernible pattern of incremental growth of periosteal bone, and the ulna possessed only a weak pattern. Growth marks were clearly evident in the shaft of the humerus and, thus, the humerus was selected for further examination. The femur also shows a strong pattern of incremental periosteal growth (Frazier, 1982) and is likely as well suited for age estimation in sea turtles as the humerus.

PREPARATION OF BONE.—The entire forelimb, usually the right, was removed, macerated in water, washed, and air-dried. Prior to sectioning, each humerus was weighed and measured (measurements are described in the following section). A transverse section of bone approximately 5–7 mm thick was cut with a bandsaw from the humerus just distal to the deltopectoral ridge. The section was stored in a 4% formalin solution for at least 24 hrs prior to decalcification.

Histological preparation began with decalcification. Several decalcification solutions were

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tried. RDO (a commercial decalcification solution) was fast and effective; however, its speed and the unequal thickness of our bone sections resulted in over-decalcification. A formic-citric acid solution was very slow and resulted in uneven decalcification. A solution of equal parts of 8% formic acid and 8% hydrochloric acid gave good results. Decalcification in the formic-hydrochloric acid solution required 4–8 days, depending upon the thickness of the bone and its porosity. Complete decalcification was determined by X-ray.

The decalcified bone was rinsed in tap water and processed in a Fisher Histomatic Tissue Processor as follows: (1) 95% ethanol for 24 hrs, three changes of alcohol, the last 12 hrs under a vacuum; (2) 100% ethanol for 30 hrs, four changes of alcohol, the last 18 hrs under a vacuum; (3) xylene for 12 hrs, three changes of xylene, all under a vacuum; (4) paraffin (paraplast) for 6 hrs, two changes, both under a vacuum. The paraffin-impregnated bone was mounted in a block of paraffin and transversely sectioned (6 μm) on a standard microtome. The bone was periodically soaked with water (cut surface of block covered with dripping wet gauze pad) to obtain the best results during sectioning. All sections were stained with Harris hematoxylin and eosin and normally differentiated.

MEASUREMENTS AND COUNTS.—When a dead sea turtle washed ashore on Cumberland Island, a series of shell and soft part measurements was collected. Only one measurement is reported here: curved carapace length (cCL), the midline distance from anterior edge of cervical scute to tips of thirteenth marginal scutes measured over the curve. Over-the-curve measurements are potentially more accurate for bloated carcasses than straight-line measurements (e.g., sCL), owing to shape changes; the measurement error increases in both types as maceration and gaseous swelling begin to separate the articular surfaces within the shell of stranded sea turtles. In spite of the potential error, these shell measurements can serve as size class designators for comparison with the nesting female loggerhead population of the Georgia coastal islands and with populations of marked-and-recaptured loggerheads from other areas.

Prior to removal of the bone section, a series of 12 straight-line distance measurements was recorded from each humerus, as well as its air dried weight. The measurements are: (1) maximum length (ML—distance from proximal-most tip of ulnar process to distal articular surface; (2) longitudinal length (LL), distance from proximal surface of head to distal articular surface, parallel to longitudinal axis of humerus; (3) ulnar process length (UPL), distance from proximal tip of ulnar process to juncture of head and process; (4) proximal length (PL), distance from proximal surface of head to distal edge of radial process, parallel to longitudinal axis; (5) proximal width (PW), distance from preaxial surface of head to postaxial surface of ulnar process, perpendicular to longitudinal axis; (6) radial process length (RPL), distance from pre- to postaxial edges of process, diagonal to longitudinal axis; (7) width at deltopectoral crest (DpCW), transverse distance of shaft from pre- to postaxial surfaces at deltopectoral crest; (8) medial width (MW), transverse distance from pre- to postaxial surfaces at point of minimum width; (9) distal width (DW), transverse distance from pre- to postaxial surfaces at juncture of articular condyles with shaft; (10) maximum head diameter (MaxHD); (11) minimum head diameter (MinHD); (12) thickness (T), minimum depth in middle of shaft, approximately in vicinity of MW, perpendicular to longitudinal and transverse axes.

The histological sections were measured grossly and microscopically. The length and width of bone sections were measured with a caliper to 0.1 mm. The periosteal layers were measured to 1.0 μm with a Wild micrometer and counted at 60 × magnification on a transmitted light microscope. The counts and measurements of the layers were made along two perpendicular axes, the long (pre-postaxial) and short (dorsoventral) axes, of the bone section.

Anatomy of the Humerus

GROSS MORPHOLOGY.—The humerus of the sea turtles (Cheloniidae and Dermochelyidae) differs from that of all other extant turtles in several respects. Presumably, the differences are related to a structural reorganization of the forelimb for aquatic flight. The sea-turtle humerus, specifically that of *Caretta caretta* (Figure 1), is flattened in cross-section as well as in the proximodistal plane. Cross-sections through most regions of the diaphysis (shaft) have elliptical outlines. The head lies at an approximately 45° angle from the diaphysis in contrast to the nearly perpendicular orientation in other turtles. The articular surface retains the 180° arc, thereby

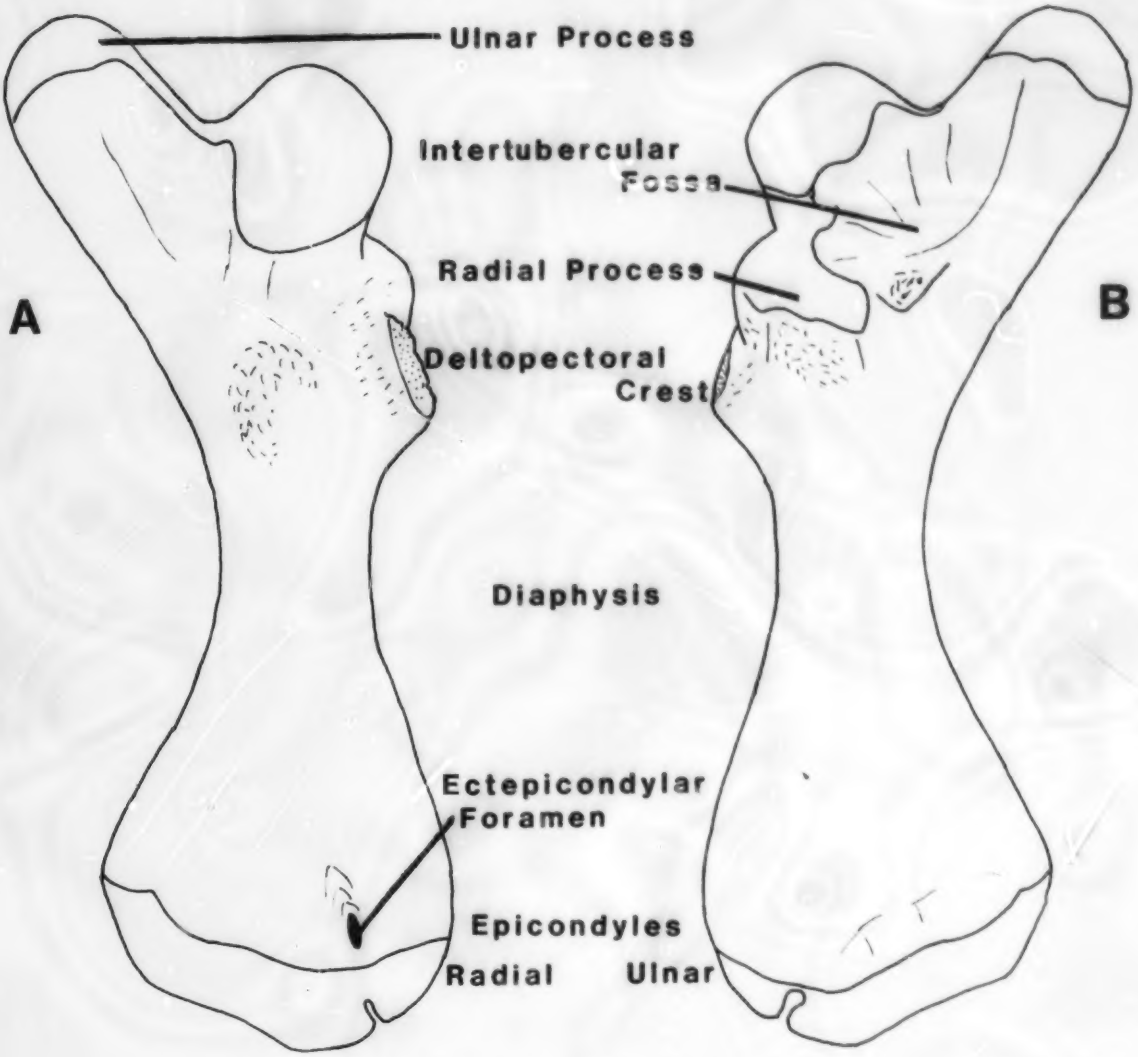

FIGURE 1.—Entire right humerus: A, dorsal view; B, ventral view.

FIGURE 2.—Growth series of humeri showing the closure of the ectepicondylar foramen through growth. Curved carapace lengths of specimens (left to right): 995, 965, 890, 815, 720, 660, and 590 mm.

giving the articulation a limited ventral aspect as well as medial and dorsal ones. In general appearance, the articular surface is egg-shaped, with the blunter end ventral and the long axis dorsoventral. The anterior articular shoulder or flange, so characteristic of the humeral head of other turtles, is absent; there is no hint of its former presence. The ulnar (medial) process (or tuberosity) is narrow and elongate, extending posteromediad at approximately a 25° angle from the shaft; the medial tip of the process is strongly proximal to the humeral head. The radial (or lateral) process lies distal to the head and ventrally on the preaxial edge of the diaphysis. The radial process is often stated (Romer, 1956:355) to have shifted distally on the shaft, yet a comparison of its position and its orientation in other turtles suggests that the change in head orientation and the elongation of the ulnar process result in a change in the radial process's relative, but not actual position on the shaft. Another process arises on the preaxial border contiguously with the radial process. This process is suitably called the deltopectoral crest owing to

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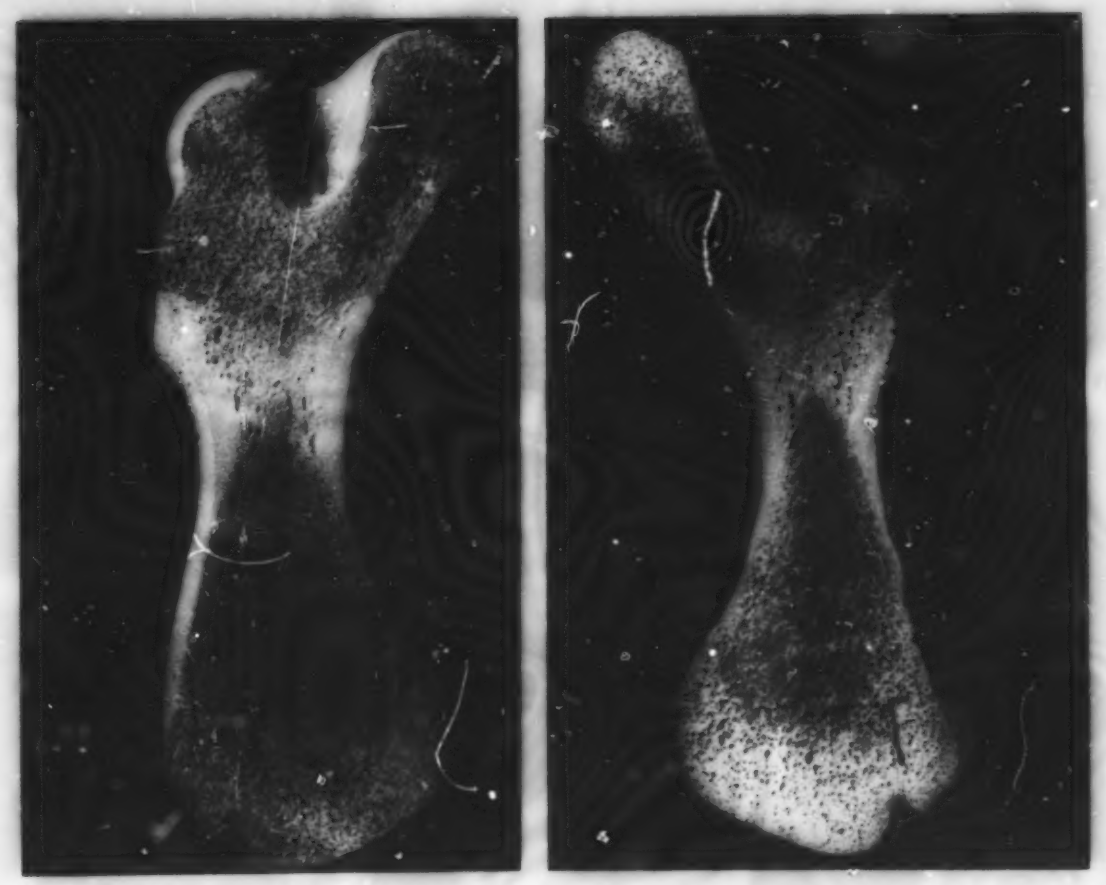

FIGURE 3.—Frontal section of the humerus: dorsal half on left, ventral half on right; 660 mm cCL.

its location in the center of the insertions of the deltoid and pectoral muscles; however, this name is used by others, such as Romer (1956), as a synonym of the radial or medial process. In sea turtles, they are clearly two distinct processes and shall be so treated in the subsequent discussion.

Immediately distal to these two processes, the diaphysis narrows and then gradually widens (along the pre-postaxial axis) distally toward the epicondyles. The epicondylar surface is smooth with only a slight medial concavity to separate the radial and ulnar epicondyles. The radial epicondyle is notched in subadults and juveniles by the ectepicondylar groove. The groove gradually closes with age as the epicondylar area grows beyond and around the radial nerve and blood vessels (Figure 2).

Externally, the humerus bears a smooth, dense bony surface except for the articular surfaces and a few of the major muscle insertions. The humeral head, the ulnar, radial and deltopectoral processes, and the epicondyles possess smooth porous surfaces. The head region of the intertubercular fossa, the region between the radial and deltopectoral process, and the dorsal surface of the diaphysis adjacent to the head are commonly rugose; other regions develop ridges or rugosities in larger (presumably older) turtles. Internally (Figures 3 and 4), the humerus consists of a narrow shell of dense compact bone and a

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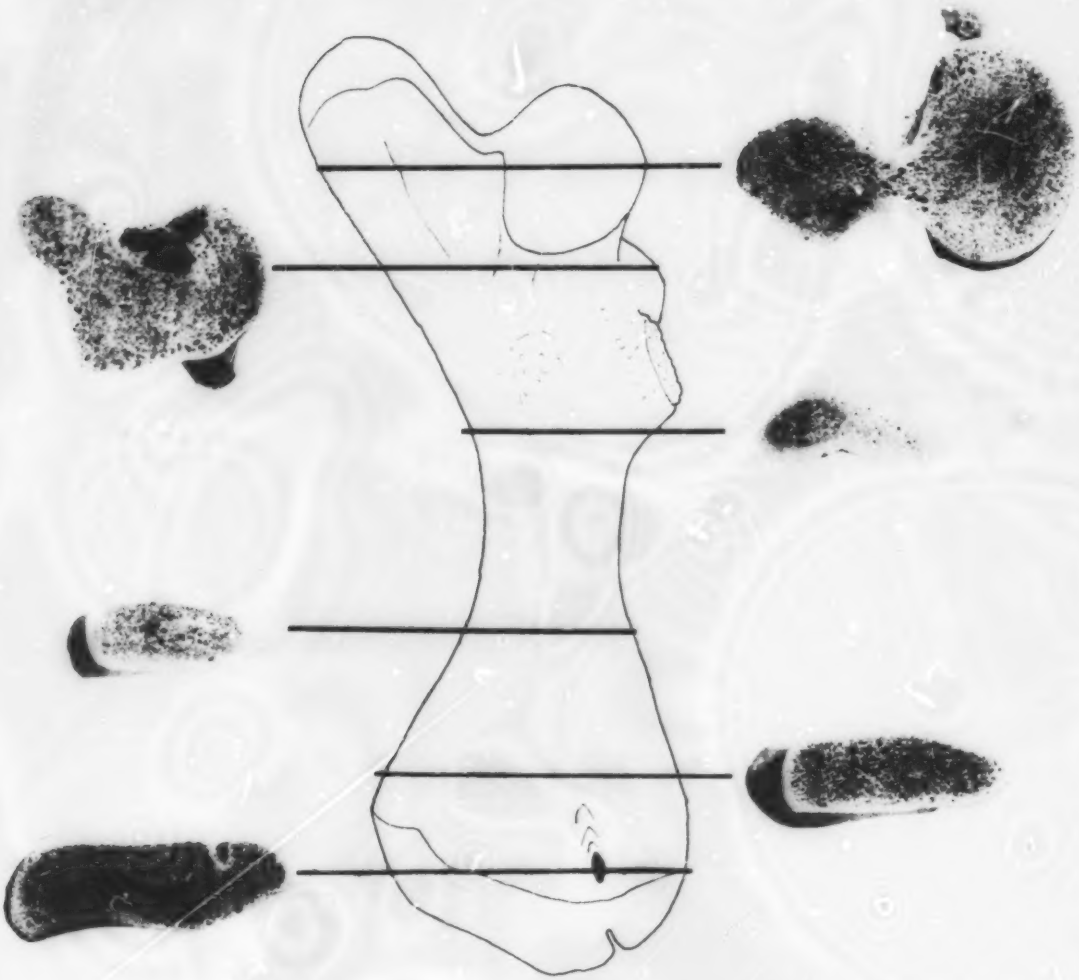

FIGURE 4.—Representative cross-sections of the humerus. The photographs show the proximal surface of each section, except for the distal-most section, which shows the distal surface.

core of spongy cancellous bone. The dense bone contains the periosteal growth layers; the spongy bone is the endosteal, remodeled periosteal, and perhaps endochondral bone. There is no marrow cavity, although the center of the bone is more porous owing to the concentration of blood vessels.

MORPHOMETRICS.—The change of the ectepicondylar groove to a foramen suggests differential or asymmetrical growth of the humerus. Comparison of a hatchling's (48 mm cCL) humerus with that of a juvenile (565 mm cCL) does show proportional changes in humerus shape (Figure 5). The present sample permits an examination of shape changes from half grown juveniles (560 mm cCL) to reproductively active adults (>900 mm cCL); however, the sample does not permit segregation by sex. We examine only a subset ($N = 80$) of the data to address the relative growth of humerus length to body length

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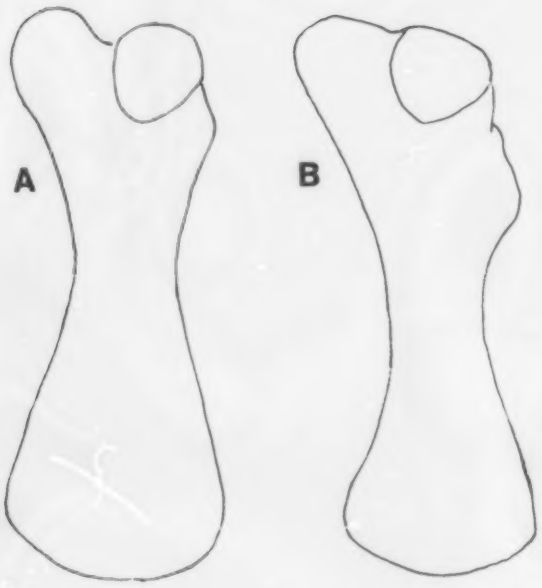

FIGURE 5.—Comparison of humerus shape in a hatchling (A; cCL = 48 mm), and an old juvenile (B; cCL = 565 mm).

and differential longitudinal growth of the humerus and some of its processes (Figure 6).

Not surprisingly, both measures of humeral length—maximum (ML) and longitudinal length (LL)—are strongly correlated to carapace length (cCL); for example, the correlation coefficient of LL/cCL is 0.98 (LL = −13.25 + 0.2033 cCL). Similarly, other humeral measurements are strongly correlated with carapace and humeral length. The two length measurements possess a nearly isometric growth pattern (ML = −6.97 + 1.1077 LL; $r = 0.996$). The regression slope is greater than 1.0, however, and suggests that the ulnar process grows slightly faster than the major axis of the humerus (i.e., the ulnar process length is contained within the ML measurement, but not within the LL measurement). The ulnar process (UPL) grows faster than the radial process (RPL), as demonstrated by a UPL/LL slope of 0.24 and a RPL/LL slope of 0.19. Although the differences in growth rate are slight, they tend to confirm the production of the peculiar configuration of the proximal end of the sea

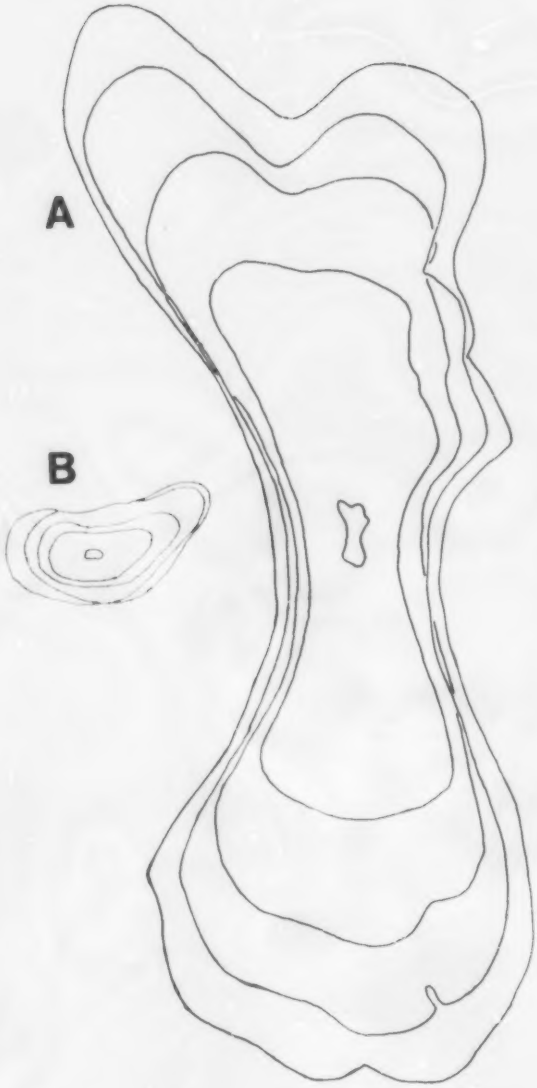

FIGURE 6.—Growth changes in humerus: A, whole bone; B, cross-section through the middle of diaphysis. The lines represent outlines from actual specimens.

turtle humerus through differential growth of the processes.

TISSUE ORGANIZATION.—The following description is based on bone that has been macerated, air dried, and hydrated in formalin prior to histological preparation; thus, only the min-

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eralized framework of the bone remains. Further, the description is based entirely on transverse sections through the diaphysis immediately distal to the deltopectoral crest, and of individuals with cCL greater than 55 cm.

The cortex and medulla are composed of cellular, vascular bone (terminology from Enlow, 1969). Both the cortex and medulla are formed by periosteal deposition. The layers are distinct in the cortex, but strongly modified in the medulla by enlargement of the blood vessels through resorption and endosteal layering of these vascular canals. The layers appear to consist entirely of non-lamellar (parallel-fibered) bone. The remodeling of the vascular canals in the cortex results in one to several layers of endosteal bone on the wall of the canal; however, we are reluctant to label the resulting structure as secondary osteones (Haversian systems), owing to the irregular spacing of the osteocyte lacunae. The endosteal layers appear to be non-lamellar bone.

The bony layers of the cortex are the growth layers used in skeletochronolgy. Each growth layer consists of a light-staining area and dark-staining area. The light area represents an area of rapid growth, the dark area slow or no growth. Together, an adjacent light and a dark area represent one complete cycle of growth; hence their pivotal importance in skeletochronology. Castanet (1982; Castanet and Naulleau, 1974; Castanet and Cheylan, 1979) has established a formal terminology for the layers and their subunits; his terminology is used here and translated into English where necessary. Each growth layer is called a mark of skeletal growth (MSG; = MSC of Castanet) and consists of a zone (broad, light-staining region) and a line of arrested growth (LAG; = LAC of Castanet; narrow, dark-staining region).

Estimation of Age

Assumptions and Difficulties.—Our primary assumption is that each MSG represents one year of growth. Tests of this assumption/hypothesis have produced conflicting conclusions, i.e., both for confirmation and falsification. Our results favor the acceptance of this hypothesis, although, as we noted earlier in the introduction, some authors (e.g., Dobie, 1971), reject this hypothesis. Hohn and Frazier (1979) recognized the presence of growth layers (MSGs) in *Eretmochelys* and the positive correlation of MSG number to shell size. To test this correlation further, Frazier (1982) examined sections of humeri and femora in five species of sea turtles. His conclusions were that (1) bone sections of *Dermochelys* and *Lepidochelys* are difficult to interpret and other sea turtles, particularly *Eretmochelys*, have readable growth layers; (2) the interpretation of growth layers in sea turtle bones is not simple, owing to endosteal resorption, unequal lamellar accretion rates, and variable visibility and routes of arrested growth lines (LAGs); (3) width of adjacent MSGs shows no predictable relationship; and (4) known-aged *Chelonia mydas* (14 mo, 18 mo, and 42 mo old turtles) from Cayman Turtle Farm, Ltd. often possess more growth layers than their age in years, but fewer layers than their age in months. Thus, Frazier's results suggest a falsification of the one-MSG/one-year hypothesis and his remarks (1982) echo those of Suzuki (1953) and Dobie (1971) in largely dismissing bone layers for age determination.

Our study of *Caretta* humeri reveals the same difficulties in MSG recognition and other ones as well; however, recognition of distinct MSGs is possible in the majority of specimens. Within *Caretta*, the major problem areas are as follows:

Resorption and redeposition. Loss of MSGs, usually the earlier ones; appearance of endosteal layers.

Accessory LAGs. The occasional presence of duplicate arrested growth lines (Figure 7B).

Absence of LAGs. Bone with homogeneous appearance, no apparent layering (Figure 7C).

Discontinuous LAGs. Arrested growth lines that do not completely encircle the circumference of the bone or lines which converge and cannot be differentiated (Figure 7D).

Irregular MSGs and LAGs. Occurrence of adjacent MSGs of strikingly different thickness and/or wavy or

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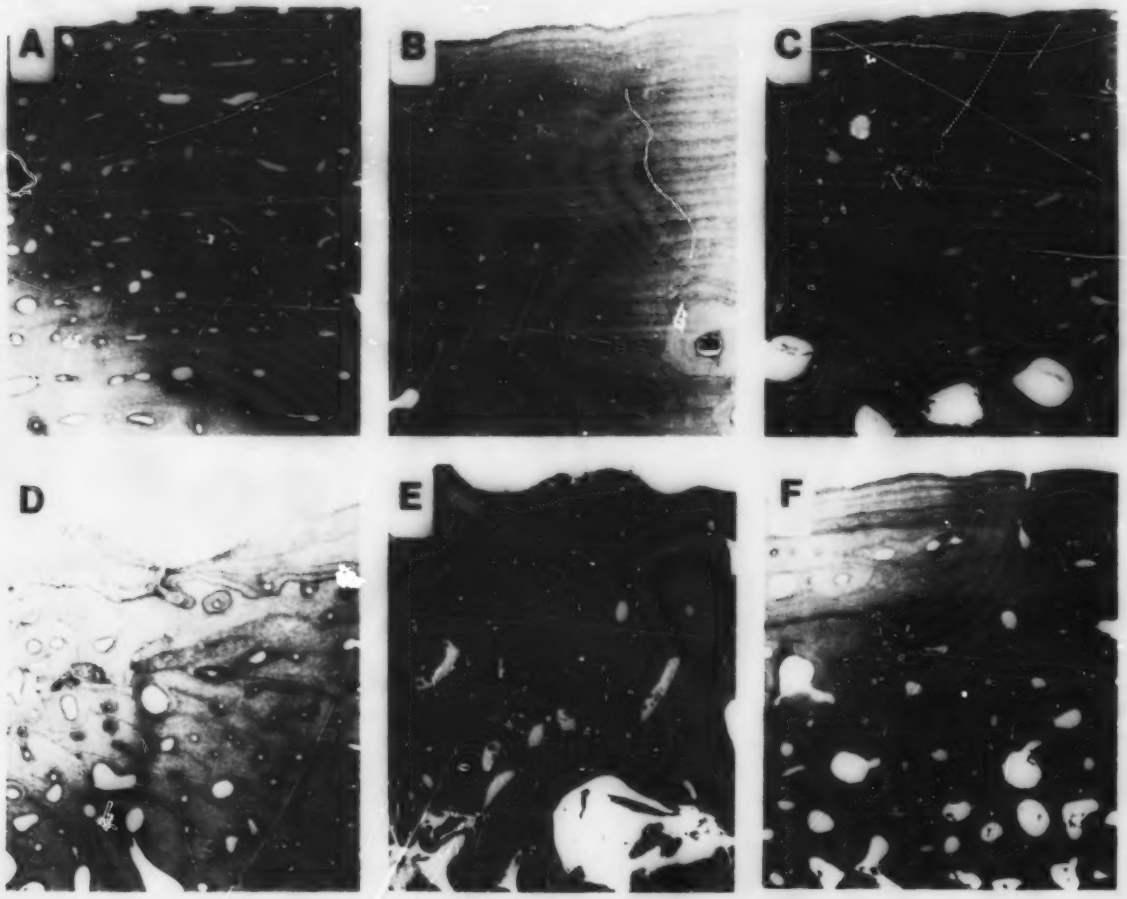

FIGURE 7.—Histological cross-sections of humeri demonstrating the various states of the marks of skeletal growth (MSGs): A, distinct MSGs bordering area of resorption; B, accessory lines of arrested growth; C, no lines of arrested growth (LAG); D, discontinuous LAGs; E, irregular growth layers; F, compaction of MSGs.

interrupted, non-contiguous arrested growth lines (Figure 7E).

Compaction of MSGs. Adjacent arrest lines so close to one another as to prevent differentiation of the individual growth layers (Figure 7F).

Resorption and redeposition of the periosteal layers is extensive in the *Caretta* humerus, because its cross-sectional diameter (narrowest axis) increases tenfold from hatching to adulthood. In addition, there are changes in proportions and in orientation of the longitudinal axis (Figure 6), thus the original humerus and the early periosteal layers are entirely replaced by remodeling and endosteal growth. The loss of the earlier periosteal layers, i.e., the MSGs, requires an extrapolation from the width of the extant MSGs in order to estimate the number of lost MSGs.

Accessory LAGs are lines probably resulting from nonseasonal retardation or cessation of growth, caused by such events as injury, illness, or short-term reduction in food supply. Often

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the accessory LAGs can be discerned from the "true" LAGs by less intense or more diffuse staining or by incompleteness of the line. Accessory LAGs potentially cause an over-estimate of age, since their development violates the one-MSG/one-year assumption.

The absence of LAGs prevents the estimation of age. The cause of this condition is unknown. Continuous, more or less uniform growth would produce this condition, although such a growth pattern seems unlikely for members of the Georgia *Caretta* population, unless some individuals migrate to warmer waters in the winter.

Discontinuous LAGs and compacted MSGs increase the difficulties of recognition of MSGs and increase the likelihood of sampling errors. They do not, however, prevent the estimation of age. Compaction is most prevalent in large turtles and may result from a reduction in growth rate following the attainment of sexual maturity (Carr and Goodman, 1970). Discontinuous MSGs may reflect a growth pattern where one region of the periosteum slowed its rate of deposition while an adjacent region did not. The process is analogous to the differential rates of deposition whereby a bone alters its shape by producing a thicker MSG (i.e., periosteal layer) on one surface than on another surface (see Figure 6 for shape changes owing to differential growth).

These problem areas cause difficulties in counting and measuring MSGs and in the estimation of age from the MSG data. These difficulties are not insurmountable, but they do require care of interpretation and impose narrow limits upon the amount of extrapolation from the age estimates. We are not proposing that we can precisely age every individual turtle. Although our age estimates may be accurate for individual turtles, our goal is to provide age estimates for various classes of turtles, e.g., immatures of 500–600 mm cCL or adults >1000 mm cCL, and most specifically to provide an accurate estimate of the age of sexual maturity for the Georgia *Caretta* population. (We assume that the juveniles living adjacent to the Georgia coastal islands become the adults breeding on these islands.) Thus, our analysis and interpretation depend upon a large sample of turtles, not on individual specimens.

We believe that such an approach overcomes the six problem areas mentioned above. First, the large sample eliminates the dependency of interpretation upon individual specimens and permits the removal of specimens with anomalous or peculiar growth patterns which would likely cause erroneous age estimates. The large sample further provides an overview of bone growth and remodeling, so that the counting and measuring of MSGs is standardized and objective. This standardization is important, because data collection is always more efficient and consistent when the collector knows the subject area well, particularly its variability, and collects the data within a limited and uninterrupted time period. The *Caretta* data set was collected by A. Wynn during a single time period (3 mo), and upon completion of the entire set, the earlier specimens and randomly selected later specimens were re-examined to confirm the consistency of the entire data set. In this latter respect, re-examination at lower magnification (10–20 ×) was useful in the confirmation of number of MSGs, although not their widths.

Such problems as accessory LAGs and irregular growth layers illustrate that periosteal growth has periods of slow and rapid growth, thereby emphasizing the cyclic nature of MSGs. Nonetheless, their presence only clouds the question of whether or not the cycle is an annual one. Our data on *Caretta* cannot address this question. Further, the inability to locate MSGs in all individuals of a sample or in all skeletal elements within a single individual is inadequate grounds to falsify the one-MSG/one-year hypothesis. We accept the annual production of one mark of skeletal growth (MSG) on several lines of circumstantial evidence.

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Our second assumption in the application of skeletochronology is that the number of MSGs lost through bone resorption/remodeling can be estimated from the number and size of the remaining MSGs. Our method depends upon using the average width of extant MSGs to estimate the total numbers of MSGs formed from hatching to death. The estimate derives from the number of times that the average MSG width occurs in half the diameter of the sample bone. The formula is

$$TM = \frac{(0.5\ BD) - HD}{AW},$$

where TM is the total number of MSGs; BD is the cross-sectional diameter of the sample bone; HD is the average cross-sectional diameter of hatchling *Caretta* humerus (HD = 1.5063 mm); and AW is average width of extant MSGs. HD is subtracted, because it represents bone diameter at age zero; only the subsequent growth marks represent years of growth. BD is halved, because the average MSG width derives from only one side of the bone.

The estimate of total number of MSGs is equivalent to age in years if we accept a cyclic growth pattern of one MSG per year and that the average width of extant MSGs accurately reflects the average width of lost and extant MSGs.

DATA ANALYSIS.—In our preliminary analysis (Zug, Wynn, and Ruckdeschel, 1983), we demonstrated a strong positive correlation of humerus length to carapace length (over-the-curve, cCL) as well as significant positive correlations of humerus length to estimated age and of carapace length to age. Those analyses are reproduced in Part 1 of the Appendix, because they provide the analytical base for our present discussion and may be unavailable to many readers of this report. Although the basic data are the same, the analytical procedure differs.

Herein, each age estimate is rounded to the nearest whole number, in contrast to the nearest hundredths in the preliminary analysis. The regression analyses examine the data in three overlapping sets: (1) IMMATURES, all specimens less than 860 mm cCL, except for individuals with excessively high estimates of age; (2) IMMATURES AND ADULTS, all specimens, except for individuals with excessively high estimates of age; (3) ALL, all specimens. The data are reproduced in Part 2 of the Appendix.

Our preliminary analysis (see Appendix, Part 1) used age as the dependent variable, because carapace and humerus length were directly measurable variables and age was estimated. That manner of presentation caused some confusion or was less easily read owing to the reversal of the axes as commonly presented for the analysis of growth. An argument can be given for each manner of presentation; hence we provide both. Importantly, the analysis of estimated age as a dependent variable provides regression equations that more accurately predict size at hatching.

A comparison of the preliminary analysis with the current analysis shows a striking difference in regression equations and correlations. (For both analyses, all correlation coefficients are statistically significant at 0.01 probability level.) The linear regression equations for both analyses (Table 1, 2L1.2; Appendix, Part 1, $N = 75$*) give unrealistic carapace lengths (407.8 and 580.5 mm, current and preliminary analyses, respectively) for hatchlings; the power or allometric equations for the same data sets (2P1.2; $N = 75$[1]) predict more realistic lengths (33.0 and 71.1 mm, respectively). Actual carapace lengths (38–50 mm; Baldwin and Lofton, 1959:342) of hatchling *Caretta* lie between these two allometric equation predictions and are somewhat closer to the current data set's prediction. The point is not that one data set is better than the other; rather that the analysis of age estimates as whole numbers versus that using decimal numbers does not alter the general results.

The age estimates derive from two axes of the humeral section. The results are usually

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TABLE 1.—Regression statistics for age estimates (long axis) and carapace length. A model code is assigned to each regression to facilitate discussion within the text. Models 1L1 and 1P1 include all specimens with cCL <860 mm except those with excessive age estimates; models 1L2 and 1P2, all specimens except those with excessive ages. Data from Part 2 of Appendix. (Abbreviations: A, Y-intercept; B, slope of regression curve; *N*, sample size; *r*, correlation coefficient.)

(X, Y)	N	A	B	r	Range X	Range Y	Model
			Linear Regression $Y = A + BX$				
Age, cCL	38	576.966	5.163	0.55	11–40	565–855	1L1.1
cCL, Age	38	−17.561	0.059	0.55	565–855	11–40	1L1.2
Age, cCL	44	615.845	3.808	0.75	11–111	565–960	1L2.1
cCL, Age	44	−77.325	0.147	0.75	565–960	11–111	1L2.2
			Power Regression $Y = AX^B$				
Age, cCL	38	402.524	0.176	0.59	11–40	565–855	1P1.1
cCL, Age	38	5.7×10^{-5}	1.966	0.59	565–855	11–40	1P1.2
Age, cCL	44	365.485	0.210	0.78	11–111	565–960	1P2.1
cCL, Age	44	1.6×10^{-7}	2.870	0.78	565–960	11–111	1P2.2

strikingly different, with the long axis yielding estimates typically two or more times those of the short axis (see Appendix, Part 2). These differences arise not from a greater number of MSGs, but from fewer MSGs of the same or narrower widths than those of the short axis. Hence, the narrower average MSG width and the greater bone diameter of the long axis result in the estimation of a greater number of MSGs, which convert to older age estimates. Because the number of MSGs seems unreasonably high and because the number of sections showing measurable MSGs on the long axis is approximately half the sample size of the short axis, the long axis data will not be emphasized.

The short axis data possess a greater uniformity of estimates, although disparate age estimates do occur between similar sized individuals and seemingly high estimates occur for other individuals. As defined earlier, the data are analyzed in three overlapping sets. The first set (IMMATURES, cCL <860 mm) contains immature turtles and is a particularly valuable set for determining the age of sexual maturity. The second set (IMMATURES AND ADULTS) includes all the turtles of the previous set and the mature turtles (cCL >860 mm). The selection of a size for classifying loggerheads as immature or mature is arbitrary, because individuals of the same sex obtain maturity at different sizes and males and females presumably mature at different average sizes. Nonetheless, a selection is useful for analysis and the 860 mm cCL should accurately sort most of the turtles in our sample. The choice of this value derives from the range of nesting-female carapace lengths, not from mean lengths which are characteristically greater than 900 mm cCL (e.g., Ehrhart and Yoder, 1978; Stoneburner, 1980). For the U.S. Atlantic coast, ranges are 845–1029 mm cCL (Cape Romain, SC; Baldwin and Lofton, 1959), 800–1150 mm cCL (Jekyll Island, Ga.; Caldwell, Carr, and Owen, 1959), 892–1186 mm cCL (Little Cumberland Isl., Ga.; Ruckdeschel unpubl. data), 830–1240 mm cCL (Merritt Isl., Fla.; Ehrhart and Yoder 1978), 775–1067 mm cCL (Hutchinson Isl., Fla.; Gallagher et al., 1972), and 749–1092 mm sCL (Melbourne Beach, Fla.; Bjorndal et al., 1983).

A comparison of age estimates from the long and the short axis samples (Tables 1 and 2) shows that the long axis sample possesses higher correlation coefficients than the short

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TABLE 2.—Regression statistics for age estimates (short axis) and carapace length. Data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

(X, Y)	N	A	B	r	Range X	Range Y	Model
			Linear Regression, Y = A + BX				
Age, cCL	68	631.009	7.460	0.49	3–25	565–855	2L1.1
cCL, Age	68	−13.454	0.033	0.49	565–855	3–25	2L1.2
Age, cCL	76	657.848	5.656	0.63	3–74	565–1010	2L2.1
cCL, Age	76	−38.976	0.070	0.63	565–1010	3–74	2L2.2
Age, cCL	81	699.103	2.149	0.60	3–175	565–1090	2L3.1
			Power Regression, $Y = AX^B$				
Age, cCL	68	529.673	0.130	0.58	3–25	565–855	2P1.1
cCL, Age	68	3.1×10^{-7}	2.616	0.58	565–855	3–25	2P1.2
Age, cCL	76	511.863	0.151	0.70	3–74	565–1010	2P2.1
cCL, Age	76	1.0×10^{-8}	3.239	0.70	565–1010	3–74	2P2.2
Age, cCL	81	537.579	0.128	0.74	3–175	565–1090	2P3.1

TABLE 3.—Regression statistics for age estimates (short axis) and carapace length. Age estimates used herein were based on the maximum number of MSGs, either observed or estimated; data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

(X, Y)	N	A	B	r	Range X	Range Y	Model
			Linear Regression Y = A + BX				
Age, cCL	68	628.010	7.553	0.49	4–25	565–855	3L1.1
cCL, Age	68	−12.550	0.032	0.49	565–855	4–25	3L1.2
Age, cCL	76	655.892	5.693	0.63	4–74	565 –1010	3L2.1
cCL, Age	76	−38.087	0.070	0.63	565–1010	4–74	3L2.2
Age, cCL	81	698.549	2.150	0.60	4–175	565–1090	3L3.1
			Power Regression $Y = AX^B$				
Age, cCL	68	519.381	0.136	0.57	4–25	565–855	3P1.1
cCL, Age	68	1.8×10^{-6}	2.349	0.57	565–855	4–25	3P1.2
Age, cCL	76	500.267	0.159	0.70	4–74	565–1010	3P2.1
cCL, Age	76	2.0×10^{-7}	3.044	0.70	565–1010	4–74	3P2.2
Age, cCL	81	530.481	0.132	0.73	4–175	565–1090	3P3.1

axis sample. This difference is especially noticeable in the linear regression analysis.

In calculating the number of MSGs for each specimen, the resulting MSG estimate was occasionally less than the number of MSGs observed. Potentially, these differences might reduce the predictability of the regression equations which were determined strictly from the MSG/age estimate data. The low frequency of higher observed MSG counts versus estimated MSG counts and the slight difference between the two when they are different have no major effect on the regression equations (Tables 2 and 3) and their curves (Figure 8C,D). The differences are sufficiently minor that the mixed data set (observed and estimated, Table 3) can be ignored.

The estimated data (Figure 8A,B) yield five estimated MSGs/ages that are clearly outside the main cluster of points. These outliers were removed from the analysis (Table 4, Figure 8E,F). Their removal results in a striking im-

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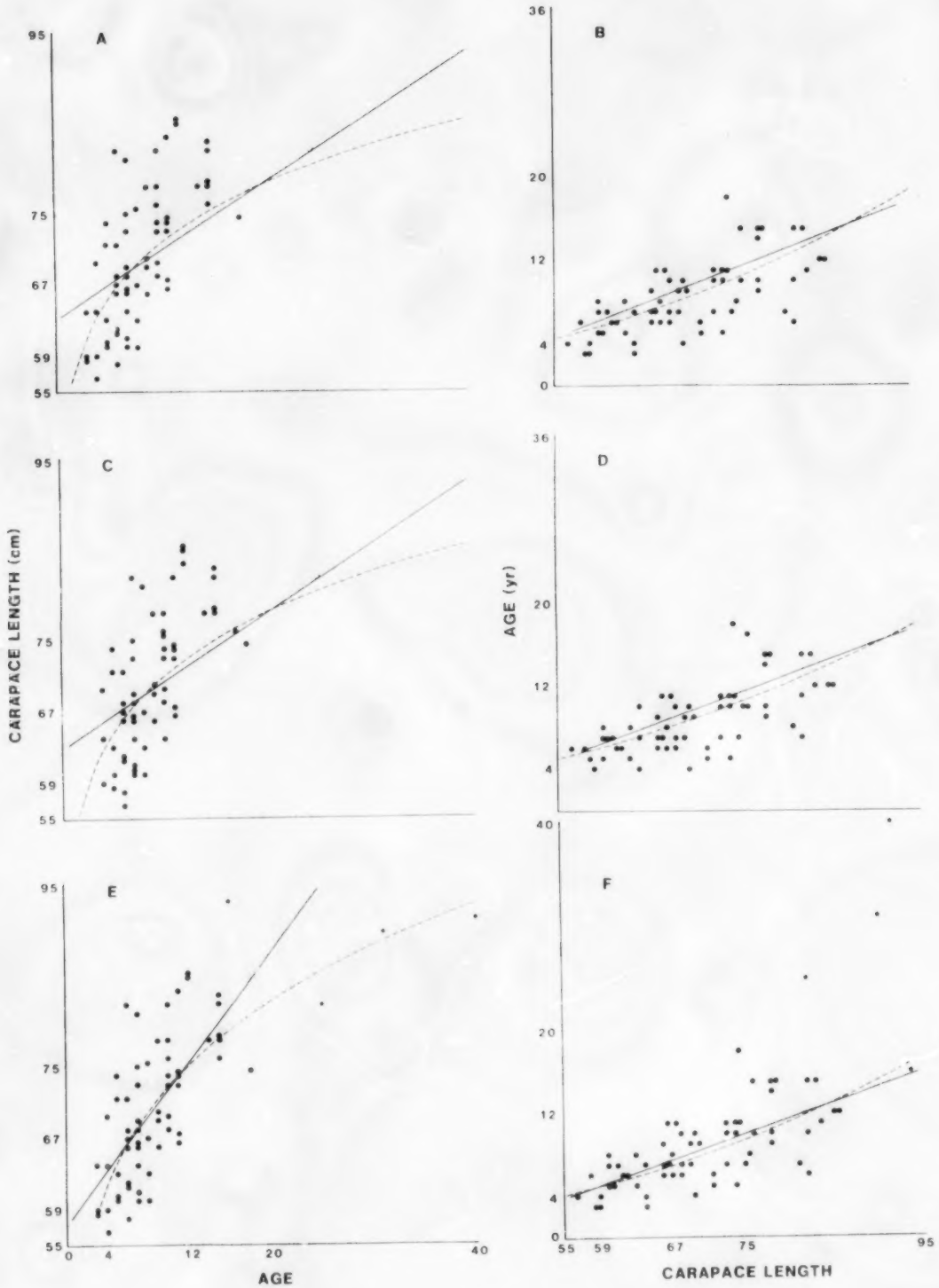

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TABLE 4.—Regression statistics for age estimates (short axis) and carapace length; same data set as in Table 2 with the removal of outliers (shown as open circles in Figure 8A,B). Data from Part 2 of Appendix. (Abbreviations and explanations same as in Table 1.)

(X, Y)					Range		
	N	A	B	r	X	Y	Model
			Linear Regression $Y = A + BX$				
Age, cCL	63	572.778	15.178	0.68	3–18	565–855	4L1.1
cCL, Age	63	−12.741	0.030	0.68	565–855	3–18	4L1.2
Age, cCL	71	656.076	5.647	0.76	3–81	565–1060	4L2.1
cCL, Age	71	−61.204	0.102	0.76	565–1060	3–81	4L2.2
			Power Regression $Y = AX^B$				
Age, cCL	63	484.290	0.178	0.68	3–18	565–855	4P1.1
cCL, Age	63	2.8×10^{-7}	2.617	0.68	565–855	3–18	4P1.2
Age, cCL	71	491.263	0.171	0.82	3–81	565–1060	4P2.1
cCL, Age	71	4.3×10^{-11}	3.972	0.82	565–1060	3–81	4P2.2

provement of the correlation coefficients and a better fit of the regression curves to the cluster of points. The outliers share no features that might explain their isolation from the other data points. They do not derive from similar-sized turtles, they do not have exceptionally high numbers of observed MSGs, and they do not have narrow average MSG widths.

The linear regressions and correlation coefficients (Tables 1, 2, and 4; Figure 8) provide reasonably good fits to the data clusters for the immature turtles (cCL <860 mm). The addition of the adult specimens to the samples (models 2L2 and 4L2) improves the correlation of carapace length with age; however, the addition of specimens with very high age estimates (e.g., model 2L3) suppresses the correlation coefficients, but not below that of the immature turtles. The same summary remarks apply to the power regressions and correlation coefficients; however, the fit is better for the power equations in all cases. Owing to the better fit and higher coefficients, subsequent extrapolation to determine body size at sexual maturity and hatching will be based on power equations. The inability of the linear regression equations to predict accurately hatchling size is apparent from the following calculations derived from the values in Table 2 where cCL(mm) and age (yr, 1 day = 0.003). For example, sizes are 631.0 mm ($Y = 631.009 + 7.46(0.003)$ for model 2L1.1), 407.8 mm ($0.003 = -13.454 + 0.033X$ for model 2L1.2), 657.9 (2L2.1), 556.8 mm (2L2.2), and 699.1 mm (2L3). Such predictions are far in excess of the 38–50 mm range for *Caretta* hatchlings (Baldwin and Lofton, 1959).

Prediction of hatchling size is improved by using the power equations. The comparable size predictions are: 248.9 mm (2P1.1), 33.4 mm (2P1.2), 212.9 mm (2P2.1) 49.1 mm (2P2.2), and 255.6 mm (2P3) from Table 2. The predictions, however, are biologically realistic only for power equations where Y equals age, which is the reverse of the typical presentation for growth. Technically, regression is appropriate only for independent variables measured without error. The age data do not meet this criterion and, statistically, are ana-

FIGURE 8.—The relationship of estimated age to carapace length. Age is an independent variable in the left column of graphs and a dependent variable in the right column of graphs. The top row of graphs (A,B) contains the ages (of immature turtles, <860 mm cCL) derived entirely from estimated MSGs (Table 2, models 2L1 and 2P1; outliers shown as open circles). The middle row (C,D) contains the ages (of immature turtles) derived from the highest number of MSGs, either observed or estimated (Table 3, models 3L1 and 3P1; outliers shown as open circles). The lower row (E,F) shows the same age data as the top row with the removal of the five outliers (Table 4, models 4L1 and 4P1).

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lyzed correctly as dependent variables. Visually, the graphs (Figure 8) show that the power curve for age as a dependent variable matches better the longitudinal axis of the data cluster for immature turtles. The better fit to the data cluster and accurate prediction also recommend the use of the power equations with age as the dependent variable.

In the determination of age at sexual maturity, linear regression and power equations show the same general pattern as observed in the hatchling-size predictions. Those equations with age as the independent variable always predict an older age than the equations with age as a dependent variable (Table 5). The skeletochronological age estimates for specimens between 801 and 900 mm cCL (Appendix, Part 2 and Figure 9) range from 6 to 31 yrs with a mean of 14.5 yrs (s = 7.4614, N = 11). These data would again recommend the use of equations with age as the dependent variable. Furthermore, the equations (both linear and power) with the closest similarity to actual data are those derived from the IMMATURE data set. Importantly, the equations $Y = (3.1 \times 10^{-7}) X\ 2.616$ (Table 2, 2P1.2; Y age, X cCL) $Y = (2.8 \times 10^{-7}) X\ 2.617$ (Table 4, 4P1.2), $Y = (1.0 \times 10^{-8}) X\ 3.239$ (Table 2, 2P2.2) yield realistic, although small estimates of hatchling size (33.4 mm, 34.7 mm, and 32.0 mm cCL, respectively). The equations $Y = 365.485 \times 0.21$ (Table 1, 1P2.1; Y cCL, $\times$ age) and $Y = 529.673 \times 0.13$ (Table 2, 2P2.2) give hatchling carapace lengths of 58.8 and 41.6 mm, respectively; these predictions are within the size range of hatchling *Caretta*. The corresponding age estimates for sexual maturity from the preceding five equations are 14.7, 13.4, 32, 58.8, and 41.6 yrs, respectively.

TABLE 5.—Age (years) at sexual maturity calculated using linear and power equations of preceding tables and an 860 mm cCL.

Data	X = Age		Y = Age	
	Linear	Power	Linear	Power
Table 1				
1L2 & 1P2	64.1	58.8	49.1	42.3
Table 2				
2L1 & 2P1	30.7	41.6	14.9	14.7
2L2 & 2P2	35.7	31.1	21.2	32.0
Table 4				
4L1 & 4P1	18.9	25.2	13.1	13.4
4L2 & 4P2	40.2	26.4	25.5	19.5

The mean age estimate for different size classes (Figure 9) shows a gradual increase in mean age from 6 yrs for the immature turtles (550–600 mm cCL) to 13 yrs for those nearing sexual maturity. The ages for the mature size classes (>850 mm) are from 20 to 50 yrs. Although the latter estimates seem biologically reasonable, the small samples for each class suggest that the data be treated with caution. This caution is also advocated by the wide range of estimates and the large standard deviations of the mature turtles. The small samples reflect not only the fewer number of adults stranding on Cumberland Island (Ruckdeschel and Zug, 1980), but also the difficulty of obtaining skeletochronological data from mature specimens. These difficulties encompass the entire spectrum from major remodeling with no MSGs to compaction of MSGs. It is the latter condition which results in the excessively high age estimates, e.g., 81 yrs for 1060 mm cCL, 142 yrs for 1000 mm cCL, 140 yrs for 975 mm cCL. These specimens have very narrow mean MSG widths, which overestimate the total number of MSGs.

Life History Implications

The preceding data center the attainment of sexual maturity on the ages of 13–15 yrs (Table 5 and Figure 9). This result matches Mendonca's (1981) estimate of 10–15 yrs for Merritt Island loggerheads remarkably well. Mendonca derived her estimates from the growth rates of recaptured wild *Caretta* with straight-line carapace lengths (sCL) of 440–925 mm. The average annual growth rate for her sample is 59 mm/yr, which yields an estimate of 13 years to reach 800 mm sCL, i.e., sexual maturity. The concordance

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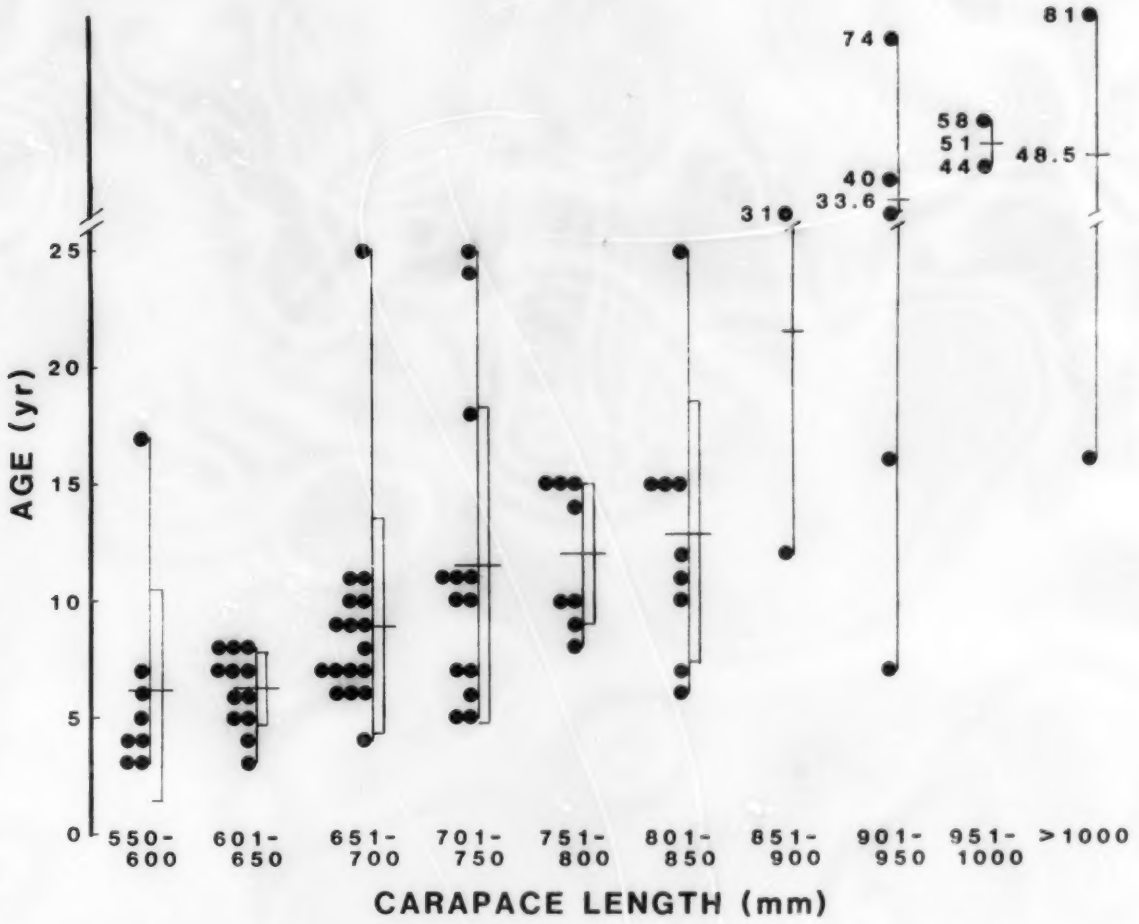

FIGURE 9.—The distributions of age estimates for sequential size classes of the 1979 Cumberland Island sample of loggerhead sea turtles. Vertical line = range; horizontal bar = mean; open box = ± 1 standard deviation of mean; each dot represents one individual.

of Mendonca's and our age estimates of sexual maturity is important in that the estimates were obtained by two strikingly different techniques; hence the concordance supports the acceptance of 15 years as an "average" age for sexual maturity of southeastern U.S. *Caretta*. Frazer and Ehrhart (1985) suggest an older "average" age for maturing loggerheads at Merritt Island. Their results derive from the Mendonca data set expanded by the inclusion of growth rates from females nesting in successive years and predict a range of 12–30 yrs for maturation. The two predictions differ for several reasons (Frazer and Ehrhart, 1985), but primarily because Mendonca used a smaller body size for determining age of maturation and a linear model (in contrast to the von Bertalanffy model) with only the faster juvenile growth rates. As noted earlier, the mean CL of nesting females is more than 900 mm. Mendonca's linear model will predict 16 yrs at this length, and our allometric equations yield ages of 16 yrs (2P1.2) and 15 yrs (4P1.2). These latter predictions are like Mendonca's, because they are derived from the IMMATURE data. Using

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the combined IMMATURE AND ADULT set, age at 900 mm cCL is 37 yrs (2P2.2) and 23 yrs (4P2.2); these latter estimates are more in agreement with those of Frazer and Ehrhart (1985). Henwood (in prep.) also uses a von Bertalanffy model and juvenile and adult growth data to predict maturation in the mid-twenties for western Atlantic loggerheads.

An earlier estimate of maturity for the Georgia *Caretta* population was 6–7 yrs (Caldwell, 1962) and was based on the growth rates of captive-reared hatchlings. The growth rate of well-fed captive sea turtles is typically two or more times faster than that of wild ones (Appendix, Part 3), and it is becoming increasingly apparent that age extrapolations from captive growth rates must be used cautiously. The average captive growth rate (from data in Appendix) is 136.6 mm/yr ($s = 35.28$, $N = 8$) for loggerheads. This rate would convert a 42 mm hatchling into an adult in 6 yrs as Caldwell (1962) and Uchida (1967) predicted. Use of captive growth rates ignores two aspects of natural growth, however. It assumes a constancy of growth rate in all growth stages, and even captive rearing of different size classes of sea turtles demonstrates the fallacy of this assumption (e.g., Frazer, 1982; Limpus, 1979; Parker, 1926, 1929; Uchida, 1967; Witham and Futch, 1977; Witzell, 1980). Furthermore, observations from captive rearing programs typically record growth from hatching to one year of age, occasionally for a second year, when growth is maximal. Second, the diet of captives is high in mass and protein and low in undigestible components (reported captive diets usually consisted of chopped fish and/or shrimp). Wild turtles probably obtain such a high quality meal rarely and probably do not approach the same mass of food on a monthly or yearly basis. Nuitja and Uchida (1982) have shown that growth rates in *Caretta* are directly linked to diet; more food produces faster growth. Third, wild turtles expend more energy in food gathering, so the net energy available for growth is presumably much less than that for captive turtles.

A striking exception to the preceding exposition are the growth data of two *Caretta* raised in captivity from hatching to 14 yrs. As they reached 14 yrs, the turtles were beginning to develop secondary sexual characteristics. If they continued their growth pattern, they would reach 860 mm cCL at 16–17 yrs and 920 mm at 19–20 yrs. Since they fed year round, although at a reduced level in the winter, an "average" age of maturation for wild loggerheads from the U.S. Atlantic coast would likely fall in the mid-twenties as postulated by Frazer and Ehrhart (1985) and Henwood (in prep.).

Most captive growth experiments demonstrate only that sea turtles are capable of rapid growth when given abundant food resources, not that they do so in the wild. The reproductive data on captive reared green sea turtles suggests, however, that the attainment of "mature" size and the production of gametes may occur prior to the animals being fully mature (Witham, 1971; Wood and Wood, 1980), because nesting frequency and clutch size of captive-reared females are well below normal. In addition, hatching success (= fertility of eggs) is extremely low the first nesting season and increases gradually thereafter (Wood and Wood, 1980). A side, but related aspect to the preceding observations is the lack of concordance between age and marks of skeletal growth (MSGs) in *Chelonia mydas* at the Cayman Turtle Farm (Frazier, 1982). Since the growth rates are abnormally high in captive turtles and this rapid growth affects the physiology of reproduction (as outlined above), the normal pattern of bone growth may be similarly disrupted; hence, captive-reared known-aged turtles are a poor basis on which to confirm or falsify the one-MSG equals one-year hypothesis.

Maturity does not occur in all *Caretta* populations at the same age. Loggerheads from the Great Barrier Reef may require more than 30 yrs (Limpus, 1979), because growth rates of the older juveniles (>500 mm CL) are only 10–20 mm/yr. Such slow growth presumably reflects the quality and quantity of the food available to these turtles rather than a genetically determined growth potential. The rapid growth response of

all sea turtle species to abundant food in captivity illustrates the plasticity of sea turtle growth. This plasticity is evident in the differential response of turtles in adjacent populations to differences in food quality and quantity. For example, *Chelonia mydas* populations in the Hawaiian Archipelago show growth rates ranging from 10 to 53 mm/yr (Appendix, Part 3), and these rates are directly correlated with food supply (Balazs, 1979, 1980, 1982; see also Gibbons, 1967; Hulse, 1976; and Parmenter, 1980 for the influence of food quality and abundance on growth in populations of freshwater turtles). *Caretta* populations may respond similarly, but the growth rates of wild populations are known for so few that such patterns cannot be discerned at present.

Growth rates and ages of maturity are not identical for all members of a population even though they may have access to the same food resources and experience the same environmental conditions. Beginning with hatching, siblings show a range of body sizes. With growth, the range/variation of body sizes increases (e.g., see Bourke, Balazs, and Shallenberger, 1977, fig. 1, for captive-reared *Chelonia mydas*). Such differential growth probably occurs throughout the juvenile stage, and Carr and Goodman (1970) have hypothesized that the variability of body size in nesting female *Chelonia* is more strongly affected by the different sizes (i.e., differential growth) attained at maturity than by differences in postmaturity growth; Hildebrand (1932) found that maturation age may differ as much as four years in sibling *Malaclemys terrapin* from the same clutch of eggs. *Caretta* should show similar variation in size and age at maturation.

Although our data cannot directly address this individuality of growth and maturity, the high variation of age estimates within size classes (Figure 9) indicates its presence. The smallest size class (550–660 mm cCL) has a range of 3–17 yrs and, excluding the 17-yr estimate, an average age of 4.6 yrs (standard deviation, $s = 1.51$). This average age closely matches the median and modal ages for this size class. With the above exclusion, this size class and the next largest (601–650 mm cCL) have the lowest variation. Age variation is noticeably higher in the larger juvenile size classes and several magnitudes higher in the adult classes (>851 mm cCL), although the sample size of the latter is too small to attribute any statistical significance to the increase in variation at maturity. The increase in variation is principally caused by the adult classes containing the full spectrum of mature individuals from those nesting for the first time to those in their fifth or later nesting season. Secondarily, the range of ages at maturity is broad, and this phenomenon is probably common to all populations of sea turtles. Even though our data are few in the mature age classes, they strongly suggest that most of the mature *Caretta* (>900 mm cCL) are old (>30 yrs). Furthermore, our data show one individual with 6 estimated MSGs and another with 25 MSGs, suggesting a potential age range of 19 yrs in maturing Georgia *Caretta*.

Our age estimates can provide estimates of growth rates in the same manner as growth rates can be used to estimate maturity. In this case, we estimate the growth by subtracting average hatchling size (45 mm) from the carapace length of each specimen and then dividing by its estimated age (short axis estimate; Appendix, Part 2). The range for the total sample is 4.2–198.3 mm/yr (Table 6) and this is equivalent to actual growth rates observed in captive and wild loggerheads (Appendix, Part 3). More important, however, is the lack of agreement with Mendonca's data (1981: table 1). Our estimates are 20–30 mm/yr faster than her observed rates. We suspect that this difference is partially explained by our inability to eliminate the earlier rapid growth from our estimates. Mendonca's data measured growth during an interval of late juvenile life; our estimates measure growth from hatching to the animal's death and include the rapid growth of posthatchlings so the average is higher. Nonetheless, the mean growth rates (Table 6) show the anticipated pattern of slowing growth with increasing size (and age). In addition, the data suggest a relatively homogeneous growth in the 650–850 mm size classes and then

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TABLE 6.—Growth rate estimates (mm/yr) for sequential size classes of loggerhead sea turtles. Sexual maturation is assumed to occur in the 851–900 mm cCL size class.

Size Class (cCL)	N*	Mean	Standard Deviation	Range
550–600	8	117.4	51.04	79.3–181.7
601–650	12	102.8	37.69	69.4–198.3
651–700	17	82.0	29.18	26.2–162.5
701–750	13	77.4	36.74	27.4–139.0
751–800	8	64.2	16.51	47.7–88.7
801–850	9	71.4	30.79	31.0–129.2
851–900	2	47.6	–	27.6–67.5
901–950	5	48.0	14.92	12.0–122.9
951–1000	2	18.4	–	15.8–21.1
> 1000	2	36.4	–	12.5–60.3

* Four specimens with extraordinary age estimates are not included in this table; their estimates are (cCL, mm/yr): 735, 4.2; 975, 6.6; 1000, 6.7; 1090, 5.9.

a sharp drop in growth with maturity (>850 mm).

In comparison to North American freshwater and terrestrial turtles (Appendix, Part 4), *Caretta caretta* appears to mature sooner than would be expected by extrapolation from ages and sizes at maturation of the smaller turtle species. The larger emydines (*Pseudemys* and *Trachemys*) and *Chelydra* typically require a minimum of 6 yrs to attain a 200 mm CL. Simple linear extrapolation would suggest a minimum of 24 yrs for maturity at 800 mm CL. The relationship between turtle species' size and their age at maturity is not linear, however, because smaller species (e.g., *Clemmys*, *Kinosternon*, and *Sternotherus* mature in 4–7 yrs at 100 mm CL or less) possess ages of maturity equivalent to those of their bigger brethren. Clearly one aspect which biases our expectation of delayed maturity is that the majority of turtles studied derive from cooler aquatic environments with shorter growing seasons than the sea turtles studied. Turtles in warmer waters do grow faster (Cagle, 1954; Gibbons et al., 1981; Thornhill, 1982), and where examined closely (Gibbons et al., 1981; Parmenter, 1980), this faster growth results from two factors: primarily, owing to the availability of more and higher quality food and, secondarily, by higher ingestion rates (likely higher assimilation rates as well) and a longer growing season. Thus, relative to the growth and maturation in these turtle populations, the growth and maturation of the Georgia *Caretta* do not deviate from the expected. Furthermore, the range of wild growth rates in sea turtles (Appendix, Part 3) and the high captive growth rates suggest that there are no real intrinsic differences in growth physiology between cheloniid sea turtles and the smaller-bodied freshwater turtles. Likewise, the larger-bodied freshwater and terrestrial turtles show similar growth rates or maturation ages as sea turtles (Appendix, Part 4). This similarity is most apparent in the giant tortoises (*Geochelone*), which have estimates of 16 to more than 30 yrs to attain sexual maturity.

Summary

The humeri of *Caretta caretta* show distinct bony layers, and these marks of skeletal growth (MSGs) are assumed to be annual records of growth. The use of the skeletochronological technique is not without difficulties, such as absence of MSGs; irregular, interrupted, or accessory arrested growth lines; loss of MSGs by bone remodeling. Consequently, we use large samples and treat each age determination as an estimate.

Two age estimates were made from each bone section removed from the diaphysis just distal to the deltopectoral ridge. One estimate derived from the long axis of the section and the other from the short axis. Remodeling occurred in all humeri and required an extrapolation from existing MSGs to estimate the total number of MSGs formed during the life of the turtle. The estimate was obtained by dividing half of the humerus diameter by the average width of the extant MSGs. Since the basic assumption is that one MSG forms each year, the total number of MSGs equals the turtle's age in years. Age estimates derived from the long axis are usually 10 or more yrs higher than those from the the short axis. Also linear and curvilinear regression equations derived from short-axis age estimates and carapace lengths calculations provide the best estimates of carapace lengths at hatching. Hence,

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short-axis age estimates are considered the most reliable.

Sexual maturity in Cumberland Island *Caretta* occurs most commonly between 13 and 15 yrs from hatching. These values derive both from the average of the age estimates for the 800–900 mm cCL size class and from the regression equations for 860 mm cCL turtles, i.e., an arbitrary minimum size for *Caretta* nesting on the U.S. Atlantic coast. This age estimate for maturity matches one estimate proposed for a Florida *Caretta* population and is 5–10 yrs less for two other estimates that use 900–920 mm sCL as the size at maturity.

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Appendix

Part 1

Table and figure from our preliminary analysis of age estimates in *Caretta* (Zug, Wynn, and Ruckdeschel, 1983) in the *Marine Turtle Newsletter*. They are reproduced to permit ready comparison with the results of the present analysis.

Age estimates, carapace lengths, and humerus lengths. Data for linear regression ($Y = A+BX$)* and power ($Y = AX^B$)† equations. Other abbreviations are: cCL, carapace length over the curve; HL, humerus length; N, sample size; r, correlation coefficient. Lengths are given in mm, age in yrs.

(X, Y)	N	A	B	r	X	Y
HL, cCL	78*	−26.759	0.230	0.97	105.5–200.8	565–1060
	78†	0.078	1.136	0.97		
HL, Age	76*	−45.738	0.416	0.75	105.5–200.8	3.0–80.9
	76†	8.8×10^{-7}	3.286	0.80		
cCL, Age	75*	−51.081	0.088	0.69	565–1060	3.0–80.9
	75†	1.0×10^{-9}	3.498	0.73		
cCL, Age	78*	−108.40	0.171	0.69	565–1069	3.0–175.3
	78†	0.6×10^{-11}	4.279	0.78		

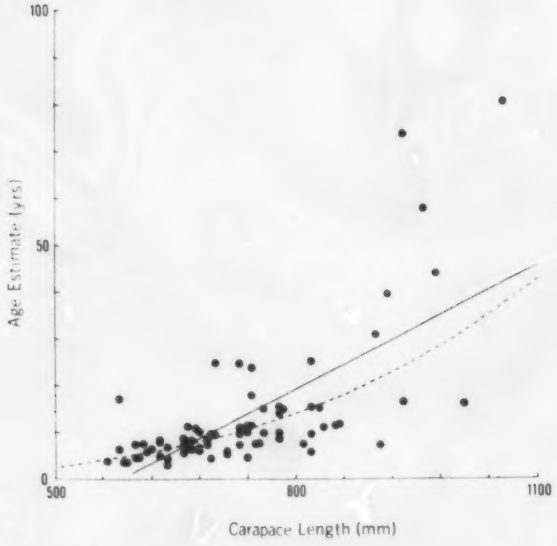

FIGURE A1.—The relation of curved carapace length to age estimates derived from periosteal annuli in *Caretta* humeri. Both the straight (linear regression) and curved (power) lines are based on 75 individuals; the three individuals with age estimates greater than 50 years were excluded from the calculations for these lines.

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Part 2

Data summary for the skeletochronological sample of *Caretta caretta* from Cumberland Island, Georgia. Age estimates were made from measurements of MSGs along the anteroposterior (long) axis and the dorsoventral (short) axis of the humerus section. Abbreviations and symbols: AW, mean width of MSGs along a single axis; cCL, carapace length over the curve; growth rate, estimated average annual cCL growth from hatching to death using estimated MSGs (short axis) as age at death; ML, maximum humerus length; †, an outlier value; *, an excessively high age estimate. The 235000 series specimen numbers are from the USNM series, from collections deposited in the National Museum of Natural History, Smithsonian Institution; the 79.0.0.0 series are field numbers assigned by the collector.

Specimen Number			Long axis		Short axis			Growth rate (mm/yr)
	cCL	ML	Obs. MSGs	Estim. MSGs	Obs. MSGs	AW	Estim. MSGs	
235284	695	123.5	–	–	4	0.76	4	162.5
235286	690	143.1	–	–	7	0.45	9	71.7
235287	960	200.8	8	111	7	0.10	58	15.8
235291	630	121.8	–	–	4	0.39	8	73.1
235292	935	198.0	–	–	9	0.10	74	12.0
235293	670	129.4	–	–	4	0.50	8	78.0
235294	665	138.0	4	35	4	0.46	11	56.4
235295	745†	146.6	11	40	17	0.20	24	29.2
235296	975	193.0	19	94	14	0.14	44	21.1
79.5.4.9	695	134.8	6	35	7	0.48	10	65.0
79.5.4.10	745	143.6	–	–	4	0.20	18	38.9
235297	700†	135.4	5	25	6	0.16	25	26.2
235298	780	154.7	–	–	4	0.42	9	81.7
235301	905	168.0	8	30	8	0.54	7	122.9
235302	740	152.4	–	–	6	0.23	11	63.2
235303	730†	144.9	4	30	9	0.20	25	27.4
235305	735*	143.5	27	343	30	0.03	164	4.2
235306	935	189.0	7	59	7	0.29	16	55.6
235310	820†	161.7	–	–	4	0.43	25	31.0
235314	1090*	250.0	23	638	41	0.04	175	6.0
235315	760	145.4	–	–	5	0.46	10	71.5
235316	1060*	224.0	10	169	18	0.10	81	12.5
235318	600	112.0	–	–	5	0.44	8	69.4
235319	820	162.1	–	–	4	0.34	15	51.7
235320	715	139.1	–	–	4	0.81	5	134.0
79.5.18.8	820	151.4	–	–	7	0.81	6	129.2
235321	900	176.6	10	89	11	0.19	31	27.6
235325	590	112.0	–	–	4	0.71	3	181.7
235327	670	132.7	–	–	4	0.58	6	104.2
235328	630	125.2	4	23	4	0.44	8	73.1
235330	850	170.3	–	–	5	0.43	12	67.1

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Part 2.—*Continued.*

Specimen Number	cCL	ML	Long axis		Short axis			Growth rate (mm/yr)
			Obs. MSGs	Estim. MSGs	Obs. MSGs	AW	Estim. MSGs	
235332	660	130.8	5	20	5	0.56	7	87.9
235333	615	119.1	6	12	6	0.79	6	95.0
235334	680	142.0	6	23	6	0.47	10	63.5
235336	820	145.6	11	24	11	0.49	10	77.5
235337	585	113.3	–	–	5	0.98	3	180.0
235338	855	157.9	9	25	9	0.50	12	67.5
235340	620	115.4	8	18	8	0.54	6	95.8
235341	640	116.2	4	12	4	1.40	3	198.3
235343	780	146.4	–	–	4	0.33	15	49.0
235344	830	159.1	7	37	6	0.35	15	52.3
235345	1010	210.0	–	–	4	0.42	16	60.3
235346	680	121.7	5	22	5	0.54	6	105.8
79.6.17.5	1000*	217.0	11	420	9	0.06	142	6.7
235348	755	141.4	11	19	10	0.50	8	88.7
235349	665	123.0	5	17	5	0.45	7	88.6
79.6.17.8	580	–	4	18	4	0.42	6	89.2
235350	835	170.2	11	35	12	0.41	11	71.8
79.7.5.1	975*	195.0	13	339	30	0.05	140	6.6
235356	730	144.4	–	–	10	0.03	10	68.5
235357	630	121.8	–	–	4	0.68	5	117.0
235358	675	129.4	5	27	5	0.35	11	57.3
235362	680	122.8	6	19	6	0.55	7	90.7
235363	730	139.9	4	20	7	0.63	7	97.8
235365	565	105.5	4	12	6	0.73	4	130.0
235366	600	123.7	–	–	6	0.50	7	79.3
235367	745	144.2	–	–	4	0.38	11	63.6
235371	660	120.0	–	–	4	0.68	6	102.5
235375	780	146.0	8	28	7	0.43	10	73.5
235378	640	131.4	6	15	7	0.66	7	85.0
235380	750	134.4	–	–	7	0.63	7	100.7
235381	915	173.5	10	43	8	0.16	40	21.7
235383	640	118.4	4	22	10	0.52	7	85.0
235388	810	156.0	5	22	8	0.73	7	109.3
235389	600	117.2	4	13	4	0.77	5	111.0
235390	830	155.5	–	–	4	0.34	15	52.3
235391	590	107.9	–	–	4	0.82	4	136.3
235392	785	147.3	4	36	5	0.35	15	49.3
235393	760	141.1	10	32	17	0.31	15	47.7
235394	730	146.0	8	23	9	0.42	11	62.3
235395	740	143.3	4	24	6	0.49	10	69.5
235397	640	119.5	–	–	4	1.02	4	148.7
235398	580†	116.3	–	–	8	0.18	17	31.5
235399	660	128.1	7	36	7	0.42	9	68.3
235400	700	124.7	4	22	4	0.45	9	72.8
235401	780	149.9	–	–	5	0.31	14	52.5
235407	715	130.0	5	13	5	0.77	6	111.7
235415	610	113.5	4	26	7	0.58	7	80.7
235417	740	133.6	–	–	5	0.87	5	139.0
235418	690	123.7	7	18	7	0.60	7	92.1
235419	605	106.5	4	11	7	0.74	5	112.0

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Part 3

Summary of selected references on growth rates and age estimates of sexual maturity in cheloniid sea turtles. The data listed below may not match the values listed in the text for these references, because we often summarized the original data; the data could not be standardized to a single method of carapace measurement. (Abbreviations: C, data from captive raised turtles; W, mark and recapture data from wild turtles; dash, no data; ?, questionable data.)

Species Locality	Sample size	Exper. cond.	Growth rate (mm/yr)	Age at maturity (estim. yrs)	Reference
Caretta caretta					
Florida	67	W	37.0	–	Bjorndal et al., 1983
Florida	2	C	82.1	–	Caldwell et al., 1955
Georgia	5	C	131.4	6–7	Caldwell, 1962
North Carolina	2	C	110.3	–	Hildebrand and Hatsel, 1927
Colombia	9	C	176.8	–	Kaufmann, 1972
Colombia	13	C	111.4	–	Kaufmann, 1972
Great Barrier Reef	–	W	–	>30	Limpus, 1979
Florida	13	W	59.0	10–15	Mendonca, 1981
Florida	1	C	161.7	–	Parker, 1926
Florida	8	C	182.9	–	Rebel, 1974
Florida	25	C	136.4	–	Witham and Futch, 1977
Chelonia mydas					
Hawaii	4	W	52.8	11	Balazs, 1979, 1982
Oahu	2	W	24.0	24	Balazs, 1980, 1982
Necker	1	W	16.8	34	Balazs, 1980, 1982
French Frigate	19	W	9.6	59	Balazs, 1980, 1982
Lisianski	3	W	15.6	36	Balazs, 1980, 1982
Midway	8	W	10.8	53	Balazs, 1980, 1982
Kure	2	W	9.6	59	Balazs, 1980, 1982
hatchlings	4	C	210.3	–	Balazs, 1980
immatures	6	C	60.1	–	Balazs, 1980
adults	8	C	0.24	–	Balazs, 1980
U.S. Virgin Islands	35	W	50.4	–	Boulon, 1983
Florida	4	C	110.0	8–13	Caldwell, 1962
Tortuguero	141	W	5.8	–	Carr and Goodman, 1970
Sarawak	–	C	104.0	4–6	Hendrickson, 1958
Colombia	4	C	148.9	–	Kaufmann, 1972
Torres Strait	8	W	17.4	–	Kowarsky and Capelle, 1979
Great Barrier Reef	40	W	13.2	>30	Limpus, 1979
Great Barrier Reef	12	W	1.4	–	Limpus, 1979
Heron Island	40	W	13.5	>30	Limpus and Walter, 1980
Florida	12	W	35.4	25–30	Mendonca, 1981
Heron Island	2	C	120.9	–	Moorhouse, 1933

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Part 3.—*Continued.*

Species Locality	Sample size	Exper. cond.	Growth rate (mm/yr)	Age at maturity (estim. yrs)	Reference
St. Thomas	9	W	51.1	–	Schmidt, 1916
Mauritania	–	C,W	–	5.5	Toquin et al., 1980
Florida	12	C	166.9	–	Witham and Futch, 1977
Grand Cayman	22	C	–	8–10	Wood and Wood, 1980
Eretmochelys imbricata					
U.S. Virgin Islands	15	W	33.6	–	Boulon, 1983
Jamaica	?	C	50.3	–	Brown et al., 1982
Jamaica	?	C	23.3	–	Brown et al., 1982
Florida	9	C	86.8	–	Caldwell, 1962
Sri Lanka	1	C	247.2	–	Deraniyagala, 1939
Sri Lanka	1	C	93.0	–	Deraniyagala, 1939
Seychelles	10	C	170.5	–	Diamond, 1976
Sarawak	3	C	113.4	4	Harrisson, 1963
Sarawak	4	C	132.1	–	Harrisson, 1963
Colombia	7	C	174.2	–	Kaufmann, 1972
Torres Strait	2	W	90.6	–	Kowarsky and Capelle, 1979
St. Thomas	3	C	192.8	–	Schmidt, 1916
Samoa	6	C	172.3	3.5	Witzell, 1980
Lepidochelys kempi					
Florida	2	C	42.0	–	Caldwell, 1962
Mexico					
juveniles	–	C	105.0	–	Marquez, 1972
adult females	>10	W	35.0	5.5	Marquez, 1972
Lepidochelys olivacea					
India	15	C	125.2	–	Rajagopalan, 1984
India	19	C	143.3	–	Rajagopalan, 1984
Sri Lanka	3	C	52.7	–	Deraniyagala, 1939
Sri Lanka	1	C	188.4	–	Deraniyagala, 1939

Part 4

Summary of selected references on minimum size and estimated ages at sexual maturity in miscellaneous freshwater and terrestrial turtles. The data listed below may not match the values listed in the references, because we may have abstracted the original data or extracted the data from graphs or figures. (Abbreviation: PL, body size given as plastron length rather than as carapace length.)

Species Locality	Minimum size at maturity (CL, mm)	Age of maturity (yrs)	Reference
Chelydra serpentina			
Iowa ♀♀	210	6–10	Christiansen & Burken, 1979
Iowa ♂♂	190	4–5	Christiansen & Burken, 1979
Quebec ♀♀	200	–	Mosimann & Bider, 1960
Tennessee	145	–	White & Murphy, 1973
Chrysemys picta			
All ♀♀	120–130 (PL)	–	Cagle, 1954
Michigan ♂♂	90 (PL)	3–4	Cagle, 1954
Illinois ♂♂	70 (PL)	2–3	Cagle, 1954
Louisiana ♂♂	50–60 (PL)	1	Cagle, 1954
Pennsylvania ♀♀	110 (PL)	5–6	Ernst, 1971
Pennsylvania ♂♂	80–90 (PL)	4–5	Ernst, 1971
Michigan ♀♀	120–130	6–7	Wilbur, 1975
Michigan ♂♂	90–105	4–5	Wilbur, 1975
Clemmys guttata			
Pennsylvania ♀♀, ♂♂	80–90 (PL)	7–10	Ernst, 1975
Emydoidea blandingii			
Massachusetts ♂♂	180–190	9–11	Graham & Doyle, 1977
Geochelone elephantopus			
hoodensis ♀♀	550	>30	MacFarland et al., 1974
hoodensis ♂♂	700	>30	MacFarland et al., 1974
porteri ♀♀	800	>30	MacFarland et al., 1974
porteri ♂♂	950	>30	MacFarland et al., 1974
Geochelone gigantea			
Malabar ♀♀	–	16–18	Swingland & Coe, 1978
Grand Terre ♀♀	–	22–24	Swingland & Coe, 1978
Kinosternon flavescens			
Oklahoma	80	5–6	Mahmoud, 1967
Kinosternon subrubrum			
Florida	80	6–7	Ernst et al., 1973
Oklahoma	80	5–6	Mahmoud, 1967
Macroclemys temminckii			
Louisiana	340–400	11–13	Dobie, 1971
Malaclemys terrapin			
N. Carolina captive ♀♀	120–140	5–9	Hildebrand, 1932
N. Carolina captive ♂♂	80–90	2–6	Hildebrand, 1932

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Part 4.—*Continued.*

Species Locality	Minimum size at maturity (CL, mm)	Age of maturity (yrs)	Reference
Pseudemys floridana			
S. Carolina ♀♀	200–240 (PL)	6–7	Gibbons & Coker, 1977
S. Carolina ♂♂	100–120 (PL)	3–4	Gibbons & Coker, 1977
Sternotherus carinatus			
Oklahoma	80	4	Mahmoud, 1967
Sternotherus odoratus			
Oklahoma	65	5–6	Mahmoud, 1967
Terrapene ornata			
Kansas ♀♀	110–120	6–11	Legler, 1960
Kansas ♂♂	100–110	4–9	Legler, 1960
Trachemys scripta			
S. Carolina: Ellent. Bay ♀♀	160–170 (PL)	7	Gibbons et al., 1981
S. Carolina: Ellent. Bay ♂	80–100 (PL)	4	Gibbons et al., 1981
S. Carolina: Par Pond ♀♀	200–210 (PL)	7	Gibbons et al., 1981
S. Carolina: Par Pond ♂♂	80–100 (Pl)	3	Gibbons et al., 1981
Illinois natural ♀♀	170–195	4–5	Thornhill, 1982
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